Genetic Diversity in California Sea Otters: Theoretical Considerations and Management Implications

Katherine Ralls, Jonathan Ballou

Department of Zoological Research, National Zoological Park,
Smithsonian Institution, Washington, DC 20008, USA

&

Robert L. Brownell, Jr

US Fish and Wildlife Service,
National Museum of Natural History,
Washington, DC, 20560, USA

ABSTRACT

The California sea otter population was reduced to a small number of animals by fur hunters in the 18th and 19th centuries. The population has partially recovered but is still threatened, largely because of its vulnerability in the event of a major oil spill. The translocation of enough animals to establish a second colony outside the present range has been suggested as a means of reducing the vulnerability of the population.

Any population that has been reduced to a small number and then allowed to increase may have lost some of its original genetic diversity. The loss of genetic diversity often results in deleterious effects, such as increased juvenile mortality and reduced fertility. It is therefore of interest to determine the degree of genetic diversity which the California sea otter population should have theoretically lost during its population 'bottleneck' and the number of otters which should be translocated in order to avoid substantial loss of genetic diversity in the new colony.

Application of some of the concepts of population genetics to the California sea otter indicates that the current population should theoretically retain a large proportion (77%) of whatever genetic diversity

existed in the original population and that a new colony resulting from the successful translocation of 50 breeding otters would retain much of the present genetic diversity after 40 years.

INTRODUCTION

The sea otter *Enhydra lutris* population of California is currently estimated at 1800 or less (Woodhouse *et al.*, 1977; USFWS, 1982). Although the population has made a remarkable recovery from over-exploitation in the 18th and 19th centuries, it is still considered threatened, largely because of its vulnerability in the event of a major oil spill along the California coast (Greenwalt, 1977). This threat was recently confirmed when lumber, spilled from a vessel off the coast of southern California, moved in a manner similar to oil and washed ashore over most of the population's range (Van Blaricom & Jameson, 1982). The likelihood of a sizeable population of sea otters surviving a major oil spill would be considerably increased if a second population could be established at a site some distance away from the coast. The draft recovery plan for the sea otter recommends that otters be translocated from their present range to other parts of their historical range (USFWS, 1982).

Any population that has been reduced to a small number and then allowed to increase will have lost some of its original genetic diversity (Denniston, 1978). The degree of genetic diversity present in the current California sea otter population is unknown, although a possible loss of genetic diversity, and hence 'adaptability', was among the concerns mentioned when the population was determined to be threatened (Greenwalt, 1977). Bonnell & Selander (1974) were unable to find any evidence of genetic diversity in the northern elephant seal, which, like the sea otter, was exploited to near extinction and subsequently recovered.

Small populations lose genetic diversity through two processes: inbreeding and random gene frequency drift due to sampling variance from generation to generation; in very small populations the two processes merge into one. Both processes lead to increased homozygosity (Kimura & Crow, 1963). In most instances, inbreeding leads to increased mortality in young animals and reduced fertility in adults. These deleterious effects have been reported for a wide range of species including insects and laboratory rodents (Wright, 1977), domestic animals (Lasley,

1978), mink (Johansson, 1961), captive ungulates (Ralls *et al.*, 1979; 1980), wild baboons (Packer, 1979) and birds (Greenwood, *et al.*, 1978).

There appear to be at least three reasons why increased homozygosity typically results in reduced survivorship and fertility (Packer, 1979). First, increased homozygosity increases the chances of detrimental recessive genes being homozygous and thus expressed. Second, the heterozygote is sometimes superior to either homozygote (heterosis). When this is true, inbred offspring will be less fit simply because they are homozygous at more loci. Third, increased homozygosity decreases the variability between offspring and thus decreases the likelihood of one of them being suited to survive a sudden change in environmental conditions.

If genetic diversity remains in the present sea otter population, the loss of much of this diversity would probably lead to the same deleterious effects found in other species. Therefore the number of otters used to establish a new population should be large enough to avoid such a loss. How much of the genetic diversity existing in the original California sea otter population might be expected to be retained in the present population? How many animals should be translocated to retain a substantial proportion of the existing diversity in the translocated population?

In this paper, we attempt to provide approximate answers to these questions by applying some of the concepts of population genetics to sea otters. Derivations of the equations used can be found in textbooks of population genetics, such as Falconer (1961) and Crow & Kimura (1970).

EXPECTED RETENTION OF GENETIC DIVERSITY IN PRESENT POPULATION

Our approach is to estimate the proportion of genetic diversity that would have been lost if the sea otter population behaved like the hypothetical ideal population of theoretical population genetics and then to refine this estimate by considering some of the ways in which the sea otter population differs from the ideal population.

In the ideal population, the breeding sex ratio is equal, mating is random, including self-fertilisation in random amount, generations do not overlap, selection and mutation are disregarded, and the lifetime number of offspring produced by individual parents has a Poisson distribution (Falconer, 1961; Crow & Kimura, 1970). Few, if any, of these

conditions are met by the California sea otter population. Fortunately, it is still possible to gain some idea of the degree of genetic diversity which may have been lost by this population by estimating its effective population size. The effective population size is the number of individuals which, if they bred according to the assumptions used for the ideal population, would gain or lose genetic diversity at the same rate as the actual population.

Equations 1, 2, 3 and 5 are based on the ideal population, in which the effective population size is the same as the actual population size by definition. We begin to explore the effect of deviations from the conditions of the ideal population with Eqn. 4, which assumes self-fertilisation is impossible, and to work towards an estimate of the effective population size of the California sea otter population with Eqn. 6.

Amount of genetic diversity remaining in a small population

If a large population is rapidly reduced to a small number of individuals, the amount of genetic diversity, or heterozygosity, remaining in the remnant population may be estimated by the equation:

$$H = (1 - 1/2N)H_0 \tag{1}$$

where H_0 is the original heterozygosity, H is the proportion of this heterozygosity remaining, and N is the number of individuals in the remnant population. Several authors have used this equation to calculate the percent of genetic diversity remaining in small populations of various sizes (Flesness, 1977; Denniston, 1978; Foose, in press). Figure 1 shows the percent of genetic diversity retained in remnant or founder populations of different sizes. The smallest possible remnant population, a single pair, should contain about 75 % of the original genetic diversity of the entire population; a population of as few as 10 animals would preserve almost all of the genetic diversity present in the original population.

In these calculations, genetic diversity is measured as variance. Denniston (1978) pointed out that rare genes, just because they are rare, do not contribute much to genetic variance and that the loss of rare genes is hardly counted in such calculations. By considering the average number of alleles remaining after a sudden reduction in population size rather than the genetic variance, he obtains a different view of the effect of small population size on genetic diversity: if a population was reduced to 50 animals and the original population was segregating four alleles at a
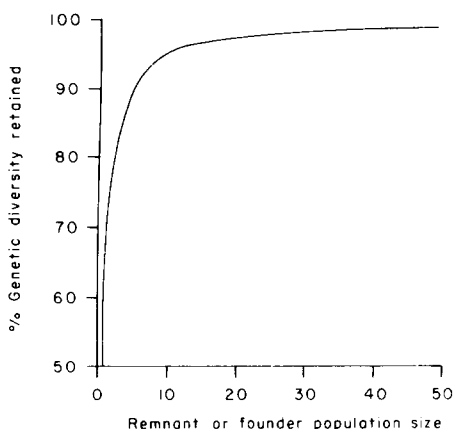
Fig. 1. The percentage of the original genetic diversity retained when a large population is instantaneously reduced to small populations of various sizes.

locus, one common (with a frequency of 0·97) and three rare, then, on the average, one of the rare alleles at the locus would be lost as a result of the population reduction.

Both models are somewhat artificial because they assume an instant reduction in population size. Still, as both approaches indicate that a quite small population will retain much genetic diversity, this conclusion seems fairly robust.

Loss of genetic diversity in small populations of constant size

Although a small population created by an instant reduction in population size will retain much genetic diversity, this diversity will rapidly be lost if the population remains small. The amount of genetic diversity lost by the population is given by:

$$H_t = (1 - 1/2N)^t H_0 \tag{2}$$

where t equals the number of generations the population has remained at size N. The percentage of genetic diversity lost in constant populations of various sizes is shown in Fig. 2. The smaller the population, the more rapidly it loses genetic diversity.

Loss of genetic diversity in populations of changing size

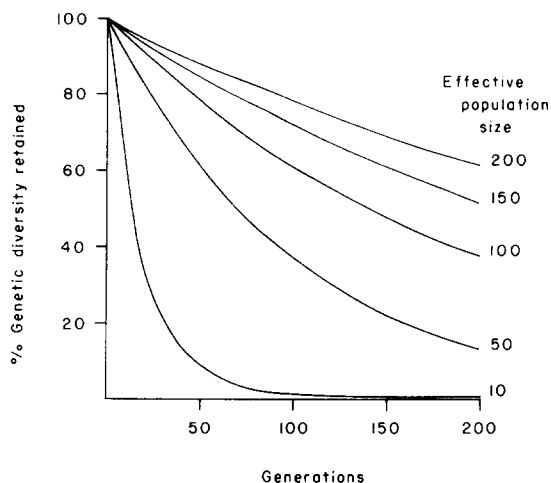When the size of a population changes over time, the harmonic mean of

Fig. 2. The rate of loss of genetic diversity in populations of various sizes.

the population sizes existing at each generation must be substituted for N in Eqn. 2 (Crow & Kimura, 1970). The harmonic mean (H_x) is given by:

$$\frac{1}{H_x} = \frac{1}{n} \sum \left(\frac{1}{x_i} \right) \tag{3}$$

where n = the number of generations in the time period under consideration, and x_i = the population size at generation i. Equation 3 is based upon the ideal population, in which mating is random, including self-fertilisation in random amount. In animals, such as sea otters, in which the sexes are separate and self-fertilisation is impossible, the percentage of genetic diversity remaining at each generation can be estimated by calculating the average inbreeding coefficient for each generation. The genetic diversity remaining at each generation is then given by one minus the inbreeding coefficient. The average inbreeding coefficient at generation t is given by:

$$f_t = \frac{1}{2N_{t-1}} + \left(1 - \frac{1}{N_{t-1}} \right) f_{t-1} + \left(\frac{1}{2N_{t-1}} \right) f_{t-2} \tag{4}$$

where N_t = the population size at generation t, and f_t = the average inbreeding coefficient at generation t (Crow & Kimura, 1970). To apply either eqn. 3 or 4 to sea otters, we must first consider the history of the California sea otter population.

History of the California sea otter population

Commercial exploitation of the population began in 1784 after the publication of the narrative of Captain Cook's voyage around the world (Ogden, 1941). Estimates of the population existing at that time range from 16 000 (CDFG, 1976) to 20 000 (A. Johnson, personal communication). Commercial hunting stopped around 1840; all legal hunting ended in 1911 with the enactment of the International Fur Seal Treaty (Ogden, 1941; Woodhouse *et al.*, 1977). Although sea otters were thought extinct in 1900, a remnant population of at least 32 was seen near Big Sur in 1914 (Bryant, 1915). The California Department of Fish and Game estimates the total population in 1914 at 50 (CDFG, 1976). Otters were 'rediscovered' in 1938, when about 50 were seen off Bixby Creek in Monterey County (Bolin, 1938). Initial reports gave the herd size as 100 to 150 otters (Fisher, 1939), although Boolootian (1961) estimated it may have been as high as 300. The population then grew rapidly; population estimates from 1914 to 1975 are summarised in CDFG (1976) and are shown in Fig. 3. Since 1973 the population size has apparently remained around 1800 animals or less (Woodhouse *et al.*, 1977; USFWS, 1982). There is no evidence that the population has increased in the last five years (Estes, 1981).

A possible time course for the decline and recovery of the population is shown in Fig. 4. The form of the curve showing the population decline is hypothetical: we assume that the population remained large during the initial stages of exploitation and then declined rapidly until the increased effort needed to capture the small remaining population resulted in a slower rate of decline.

The original population may have been divided into subpopulations, for example, on the Channel Islands and on the mainland coast. Three subpopulations, southeast of Prince William Sound, Alaska, did exist after the end of the exploitation period, one at the Queen Charlotte Islands, Canada, one in central California, and one at Islas San Benitos, Mexico (Estes, 1981) but it is known that the existing California population developed from only the central California remnant (Boolootian, 1961) and that the other two became extinct. The extent to which subpopulations would have differed genetically depends on many factors such as their size, the amount of migration between them, the degree of difference and hence selective pressures between their environments, and the fitness of homozygotes relative to heterozygotes (Chesser
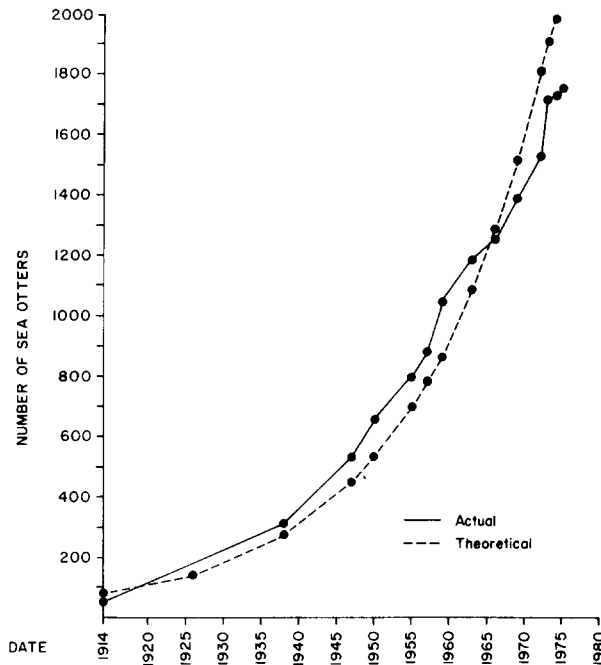
Fig. 3. Growth of the California sea otter population since 1914. 'Actual' values are CDFG estimates. The theoretical curve was obtained by fitting a linear regression to the natural log transformations of the 'actual' population estimates. The 'actual' values are above the theoretical curve during the early part of the growth period and below it thereafter.
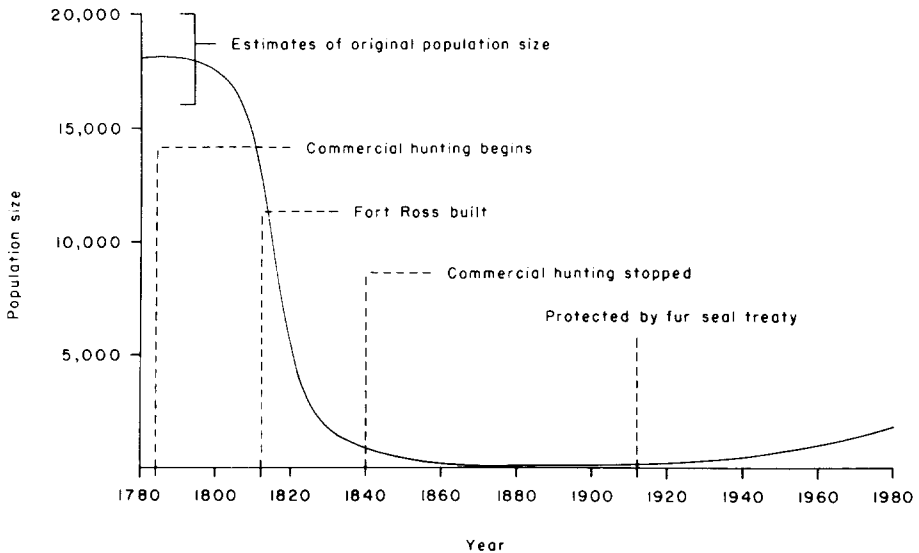

Fig. 4. History of the California sea otter population.

et al., 1980). Since it is not known whether subpopulations existed in the original population, we have modelled the California sea otter population as a single randomly mating group. This seems reasonable since observations of tagged otters in California indicate that male sea otters often make long-distance movements (R. Jameson, unpublished data). For example, the US Fish and Wildlife Service (USFWS) has tagged 42 male otters since July 1978. Eighty-nine percent of the males tagged in 1978 and 1979 have been resighted; 52% of these have made long-distance movements ranging from 64 to 97 km. If only males re-sighted during both summer and winter months are considered, the percentage travelling long distances increased to 84. One adult male tagged by the USFWS in 1978 was recovered 145 km south of the tagging location within a few months of the initial capture and a subadult male tagged by CDFG in 1978 was recaptured 161 km north of the tagging location in 1980 (Anon., 1980). As the entire range of the population is only 325 km in length, the latter animal travelled over nearly half the range.

Estimation of genetic variability remaining in the population

The information needed to apply equations 3 and 4 is the number of sea otter generations that have occurred since 1784 and the population size at each of these generations. The length of a generation is defined as the average age of the parents, both male and female, of each generation at the time the young are born (Falconer, 1961). The length of a sea otter generation is unknown. Schneider (1972) found that female sea otters in Alaska became sexually mature at three or four years of age, depending upon the locality. Females first give birth in Alaska at four to five years of age. Less information is available on the California population. The youngest female observed breeding by USFWS personnel was approximately $2\frac{1}{2}$ to 3 years old, which would make her 3 to $3\frac{1}{2}$ years old at the birth of her first pup (R. Jameson, personal communication). However, it is not known if this female actually conceived. Males become sexually mature at about seven years in Alaska (Schneider, 1972). On the basis of a much smaller sample, Green (1978) concluded that males may become sexually mature at about five years in California. However, males are probably not reproductively successful until they acquire a territory at a somewhat later age. Territorial males have not been aged, but most are large, and presumably older than the average male in the population. It

has been estimated that males do not become territorial in Alaska until 8 to 10 years of age (A. Johnson, personal communication).

A sea otter generation could not be less than the age when females first give birth and must be greater than this age because many females presumably give birth several times during their lifetime and all the male parents are likely to be more than four years of age. If the average age of the female parents were 5 years and the average of the male parents were 10 years, the length of a generation would be $7\frac{1}{2}$ years. We have used generation lengths of 4, 8, and 10 years in our calculations.

Values taken from the hypothetical rate of decline of the population shown in Fig. 4 were used as population sizes for the generations falling between 1784 and 1816. Population sizes for generations from 1914 to 1980 were based on the estimates in CDFG (1976); these data are also contained in Woodhouse *et al.* (1977) and USFWS (1982). The number of individuals present during the population's 'bottleneck' and the duration of this bottleneck are unknown. We therefore calculated the theoretical effect of a variety of bottlenecks. The minimum population size was set at 10, 25, and 50 and maintained at each of these levels for 10, 20, and 30 years. The end points of the bottlenecks for minimum population sizes of 50, 25, and 10 were determined by fitting an exponential growth curve to the population estimates given by CDFG (1976) (Fig. 3) and extrapolating this curve backward in time until these population sizes were reached in 1907, 1895, and 1878, respectively. Assuming these bottlenecks were maintained for 10, 20, and 30 years, the beginnings of the bottlenecks could be calculated by subtracting 10, 20, and 30 years from these dates. The rate of population decline from an estimated 9000 in 1816 was assumed to be exponential.

The harmonic mean population sizes obtained by substituting our assumed values for generation length, minimum population size, and duration of bottlenecks in eqn. 3 are shown in Table 1. The amount of genetic diversity remaining in the present population is directly related to the harmonic mean population size. Figure 5 shows the genetic diversity retained assuming 4, 8, and 10 year generations for the range of harmonic mean population sizes in Table 1. The proportion of the original genetic diversity one would expect to find in the present population increases with generation length.

Although eqn. 3 assumed that self-fertilisation can occur, it gives a good approximation to the results obtained with eqn. 4, which assumes separate sexes. For example, consider the extreme points in Table 1: a
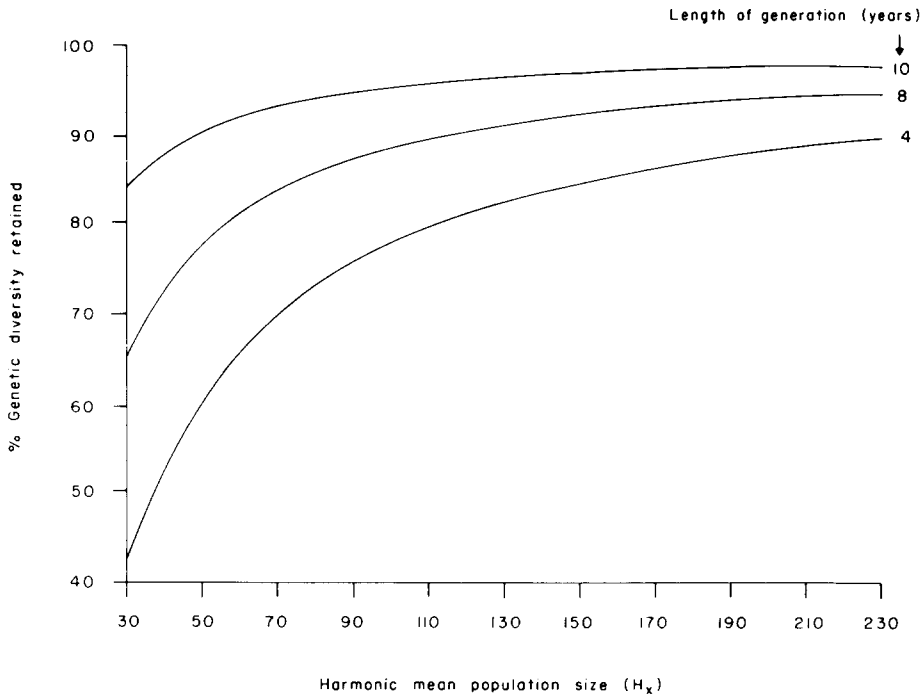
Fig. 5. The percentage of the original diversity which would be retained in the present California sea otter population for three hypothetical generation lengths in populations with various harmonic mean sizes.

generation length of 4 years and a minimum population size of 10 maintained for 30 years and a generation length of 10 years and a minimum population size of 50 for 10 years. Equation 3 yields values of 0·51 and 0·96 for these two cases whereas eqn. 4 yields values of 0·52 and 0·96.

The effective population size of the California sea otter population

Unlike the ideal population, generations in the California sea otter population overlap. Emigh & Pollak (1979) derived an expression for the effective population size of a diploid species with separate sexes and overlapping generations. We were unable to apply their formula to sea otters, as it requires a life table, which is not available for sea otters. However, they show that the usual formulas for populations with non-overlapping generations can be extended to populations with overlapping

TABLE 1

Harmonic Mean Population Sizes (H_x) from 1780 to 1980

Generation length (years)	Number of generations (t)	Bottleneck duration (years)	Minimum population size			t/H_x for Minimum population sizes of		
			50	25	10	50	25	10
4	50	10	229	125	55	0·22	0·40	0·91
	50	20	193	104	45	0·26	0·48	1·11
	50	30	167	88	38	0·30	0·57	1·32
8	25	10	229	125	55	0·11	0·20	0·45
	25	20	194	104	45	0·13	0·24	0·56
	25	30	166	89	38	0·15	0·28	0·66
10	20	10	230	127	55	0·01	0·16	0·36
	20	20	194	105	45	0·10	0·19	0·44
	20	30	168	90	37	0·12	0·22	0·54

generations if the generation times for the two sexes are the same. Although the generation time for male sea otters is probably longer than that for females, we assumed that they were the same for the purposes of estimating effective population size and used the expressions for non-overlapping generations.

Some estimates of the effective population size of a sea otter population of 100 individuals under various assumptions regarding the breeding sex ratio and variance in lifetime family size are shown in Table 2. The size of the parental generation is set at 100 individuals in all models. It must be noted that this number, N_0, refers to the number of breeding individuals in one generation and therefore cannot be obtained simply by counting the number of otters present.

Model I represents the ideal population: the breeding sex ratio is equal and the variance in family size approaches a Poisson distribution. Because the ideal population remains constant in size, each female is assumed to produce an average of two surviving pups during her lifetime. By definition, the effective population size, N_e, should equal the actual parental population size, N.

In this case,

$$N_e = \frac{(N)(\bar{K}) - 2}{\bar{K} - 1 + \dfrac{V_k}{\bar{K}}} \tag{5}$$

where N_e = the effective population size, N = the number of parents, $\bar{K}$ = mean number of successful gametes per parent, and V_k = variance of number of successful gametes per parent. Since variance in family size approaches a Poisson distribution,

$$V_k = \bar{K}\left(1 - \frac{2}{N}\right)$$

Models II to VIII are also based upon eqn. 5 but various methods are used to calculate V_k.

Model II illustrates the effect of eliminating variance in family size ($V_k = 0$). If each animal produces exactly two offspring, the effective population size is about double the actual population size. This model has little relevance to wild populations, however, because family size variation could only be eliminated under controlled breeding conditions in a captive colony.

TABLE 2

Estimates of Effective Population Size for a Sea Otter Population of 100 Breeding Individuals Under Various Assumptions Regarding Sex Ratio and Variance in Family Size

Model	Assumptions	Number of parents N	Number of ♀ parents $N♀$	Number of ♀ parents × average number of pups per ♀	Number of pups N_1	Number of ♂ parents $N♂$	Number of ♂ parents × average number of pups per ♂	Number of successful gametes	Mean number of successful gametes per parent $\bar{K}$	Variance of number of successful gametes per parent V_k	Effective population size N_e
I	Equal sex ratio Variation in family size approaches Poisson	100	50	50 × 2	100	50	50 × 2	200	2	1·96	100
II	Equal sex ratio No variation in family size	100	50	50 × 2	100	50	50 × 2	200	2	0	198
III	Sex ratio 1♂:3♀ Variation in family size approaches Poisson distribution	100	75	75 × 2	150	25	25 × 6	300	3	5·60	75
IV	Sex ratio 1♂:5♀ Variation in family size approaches Poisson distribution	100	83	83 × 2	166	17	17 × 9·3	332	3·3	9·35	54
V	Sex ratio 1♂:9♀ Variation in family size approaches Poisson distribution	100	90	90 × 2	180	10	10 × 18	360	3·6	26·24	36
VI	Sex ratio 1♂:3♀ Variation in family size as shown	100	75	65 × 2 10 × 1	140	25	3 × 14, 18 × 5 4 × 2	280	2·8	5·40	75
VII	Sex ratio 1♂:9♀ Variation in family size as shown	100	90	77 × 2 13 × 1	167	10	1 × 24, 7 × 19 2 × 5	334	3·3	23·58	35
VIII	Sex ratio 1♂:9♀ Variation in family size as shown	100	90	77 × 2 13 × 1	167	10	1 × 35, 3 × 20 6 × 12	334	3·3	24·94	34

Models III, IV, and V illustrate the effect of unbalancing the breeding sex ratio, again assuming that family size variation follows a Poisson distribution. Sea otters are known to be polygamous and fewer males than females participate in breeding. Assuming a breeding sex ratio of one male to three females reduces the effective population size from 99 to 75; assuming a sex ratio of one male to five females reduces it to 54; and assuming a sex ratio of one male to nine females reduces it to 36.

For these three models:

$$V_k = \frac{N\delta}{N}(V_k\delta) + \frac{N\female}{N}(V_k\female) + \left(\frac{N\delta}{N}\right)\left(\frac{N\female}{N}\right)(\bar{K}\delta - \bar{K}\female)^2 \qquad (6)$$

where $V_k\delta = \bar{K}\delta(1 - 2/N\delta)$ and $\bar{K}\delta = N_1/N\delta$, with corresponding formulas for females.

Models VI, VII, and VIII explore the effects of replacing the assumption that variation in family size follows a Poisson distribution with three other hypothetical patterns of family size variation. In these models,

$$V_k = \frac{\sum(K - \bar{K})^2}{N}$$

Our calculations to this point have assumed that all otters present in the population participate in breeding. This is obviously unrealistic: some proportion of the population must be immature. This proportion is unknown but a rough estimation can be made. The current population is probably 1800 animals or less; this estimate does not include dependent pups. It has long been thought that sea otters gave birth every other year (Kenyon, 1969) but recent evidence indicates that some females are capable of giving birth every year (Jameson & Johnson, 1979). However, the proportion of females giving birth at one-year intervals is not known. If most females give birth every two years, about 300 pups would be born each year (R. Jameson, personal communication). If a substantial proportion of the females give birth each year more than 300 pups would be born. Miller (1980) suggested that as many as 400 pups may be born each year.

Juvenile mortality rates in the California population may have been low when the population was rapidly expanding and may now be increasing, at least in the centre of the range, where some believe the population is at carrying capacity (Miller, 1980). Kenyon (1969) found

that 60 to 70% of the dead animals found on beaches at Amchitka, Alaska, were immatures once the population reached carrying capacity.

Juvenile mortality is probably highest during the first year of life. If 300 pups are born each year and half of them die before they are 1 year old and 20 more die each year before the females give birth at age 4, the population would contain $300 + 150 + 130 + 110$ or 690 animals less than 4 years old. Possible numbers of immature males 4, 5, and 6 years old might be 45, 40, and 40, respectively. Summing up over all age classes, we estimate that $815/1800 + 300$ or 39% of the population is immature.

Twenty percent of animals captured by the USFWS in California were subadults (R. Jameson, personal communication). Schneider (1972) found from 8 to 26% subadults in Alaskan harvests from several localities. However, both of these samples probably underestimate the percentage immatures because small pups are rarely captured. Kenyon (1969) found that 41% of the population at Amchitka, Alaska, was subadult.

We assume for working purposes that the percentage immatures in the population might range from 30 to 50%.

The presence of immature animals in the population, departures from a 1:1 breeding sex ratio, and variation in family size exceeding that expected from a Poisson distribution all act to reduce the effective population size. Table 3 shows the effective population size of an observed population of 100 animals under possible combinations of these variables.

TABLE 3

Combined Effects of Percentage Immature Animals in the Population and Variations in Breeding Sex Ratio and Family Size Shown in Table 2 on Effective Population Size. The Values in the Table Represent the Effective Population Size of an Observed Population of 100 Animals Under the Possible Combinations of Conditions

Breeding sex ratio and variation in family size according to model	Percent immature animals		
	30	40	50
I	70	60	50
III & VI	53	45	38
IV	38	32	27
VI, VII, VIII	25	21	18

The additional loss of heterozygosity resulting from the assumption that the effective population size is only some fraction of the observed population size is given by:

$$AL_{N_e} = \frac{H_{N_e}/N}{H_N} = \frac{\left[1 - \dfrac{1}{2(N_e/N)(N)}\right]^t}{\left(1 - \dfrac{1}{2N}\right)^t} \tag{7}$$

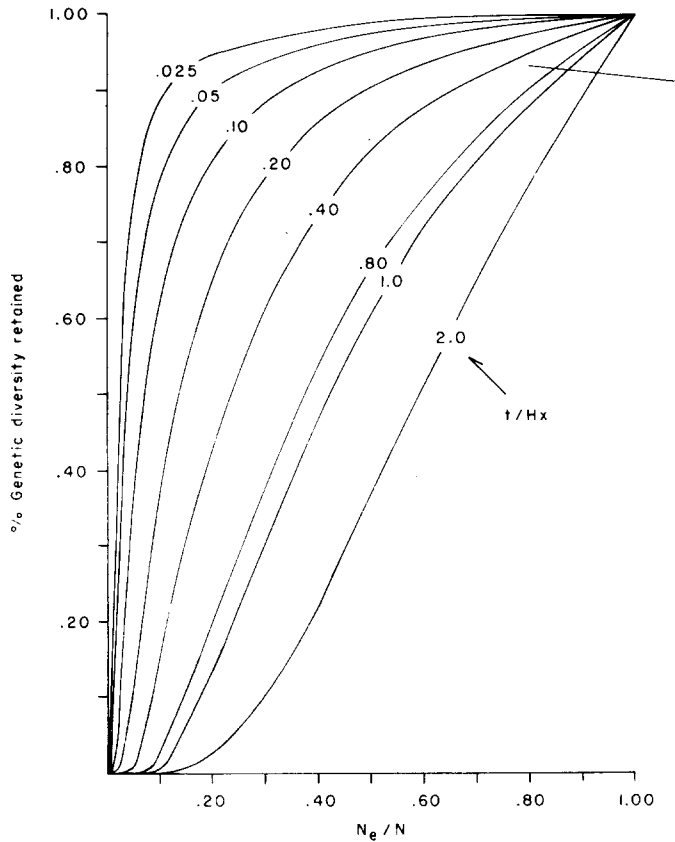where H_N = the loss of heterozygosity assuming N_e equals some fraction of N.

Fig. 6. The additional loss of heterozygosity when the effective population size is less than the actual population size. N_e/N is the ratio of the effective population size to the actual population size and t/H_x is the number of sea otter generations which are assumed to have occurred from 1780 to 1980 divided by the harmonic mean population size during the same period, as in Table 2.

Reducing, we find that AL_{N_e} decreases as a function of both t and N:

$$AL_{N_e} = \left(\frac{2N - \dfrac{1}{(N_e/N)}}{2N - 1} \right)^t \tag{8}$$

The curves can be approximated by t/N for the range of values we are considering (Fig. 6).

The interaction of assuming that N_e equals some function of N with the effects of various assumptions as to generation length, bottleneck duration, and minimum population size can be determined from Tables 1 and 3 and Figs 5 and 6. For example, if we assume Model III is correct (sea otters have a breeding sex ratio of one male to three females and variation in family size follows a Poisson distribution) and that the population contains 40 % immature animals, $N_e/N = 0.45$ (Table 3). Assuming a generation time of 8 years, a minimum population size of 50 animals, and a bottleneck lasting 10 years, we find that the harmonic mean population from 1780 to 1980 was 229 animals and $t/H_x = 0.11$ (Table 2). The percentage heterozygosity remaining in 1980, if we assume that $N = N_e$, is about 94 (Fig. 5). From the intersection of a line through $N_e/N = 0.45$ and the curve for $t/H_x = 0.1$, Fig. 6 indicates that the additional loss of heterozygosity would be about 6 %. The total percent heterozygosity remaining in the population would equal 94 % × 0.94 or 88 %.

NUMBER OF OTTERS WHICH SHOULD BE TRANSLOCATED

Jameson *et al.* (1982) reviewed possible reasons for the success or failure of past translocations of Alaskan otters. One reason for failure appears to be small population size; furthermore, many otters soon disperse from the release site and are probably lost to the breeding population at the new location. Jameson *et al.* (1982) suggest that 25–50 otters per year might have to be translocated for a period of 3–5 years in order to establish a new population. Assuming that the present California sea otter population has some genetic diversity, would such a translocation be large enough to avoid losing a substantial proportion of it?

Assume that the translocations result in a population of 50 otters established in the new location and that this population increases in the way the present population increased from a population of about 50 in

1914. The recovery of the sea otter population in California, based on the population estimates in CDFG (1976) is shown in Fig. 3. It can be seen that the actual growth rate of the population was very close to that given by the theoretical exponential growth rate:

$$N_0 e^{rt} \tag{9}$$

with r = 0·0547. Figure 3 shows a best fit of this theoretical growth rate to the CDFG estimates. (The predicted population size in 1914 is about 71 animals, which is somewhat larger than the CDFG estimates.)

After 40 years, our new population will consist of 446 animals. The harmonic mean population for this period is about 150, regardless of the length of a generation. Figure 7 shows the loss of genetic diversity assuming 4, 8, and 10 year generations and that the effective population size is equal to the number of individuals in the population.

The effects of assuming that the effective population size is various percentages of the number of individuals in the population can be determined from Figs 6 and 7. For a generation time of 4 years, $t/H_x = 0·067$ and for 8 and 10 year generations it is 0·033 and 0·027,
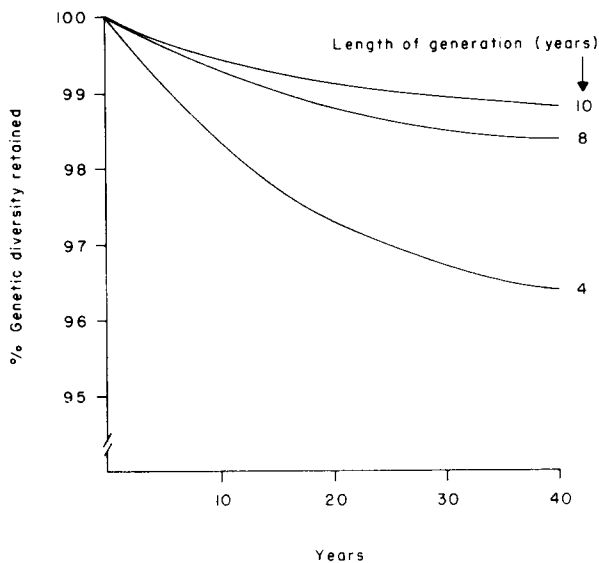

Fig. 7. Percentage of the genetic diversity present in the existing California sea otter population which would be retained in a closed translocated population after forty years for three hypothetical generation lengths, assuming the translocated population increased at the same rate as the present California population did during its recovery from overexploitation.

respectively. For example, if we assume the worst of our theoretical cases, $N_e = 0.18N$ and a four year generation time, our transplanted population would have theoretically retained about 77 % of the genetic variability existing in the founding population of 50 animals after 40 years. A more reasonable set of assumptions might be that $N_e = 0.32N$ and that the generation time is eight years. In this example our transplanted population would have retained about 86 % of the variability existing in the present California population.

DISCUSSION

In an ideal population that increases rapidly in size after going through a 'bottleneck', the reduction in average heterozygosity is rather small, even if the bottleneck size is extremely small (Nei *et al.*, 1975). The California sea otter population increased rapidly after being reduced to a small number, and thus should retain much of its original heterozygosity. Nei *et al.* (1975) point out that a small bottleneck should theoretically have a much greater effect on the number of alleles per locus than on the average heterozygosity. The California sea otter population may have lost rare alleles at some loci, but this would be difficult to detect through electrophoretic studies because of the very large sample sizes needed to detect rare alleles (Harris *et al.*, 1974).

Our model is very sensitive to generation length. If generation length is 10 years or more, even the most extreme assumptions regarding minimum effective population size (10 animals) and length of bottleneck (30 years) result in a theoretical loss of less than 15 % of the original genetic diversity in an ideal population (Fig. 5). Better estimates of generation length should be possible in the foreseeable future, as present field studies in both California and Alaska should yield data on the average age of male and female parents.

Based on currently available data, we believe a generation length may be about eight years. Given a generation length of eight years, the maximum possible loss of genetic variability in an ideal population would theoretically be about 30 % (Table 2 and Fig. 5). However, we doubt that the population size ever dropped below 50 animals and believe that the count of 32 in 1914 (Bryant, 1915) was probably an underestimate of the population existing at that time, due to lack of intensive census efforts. The best fit of the theoretical growth curve to the CDFG estimates (Fig. 3)
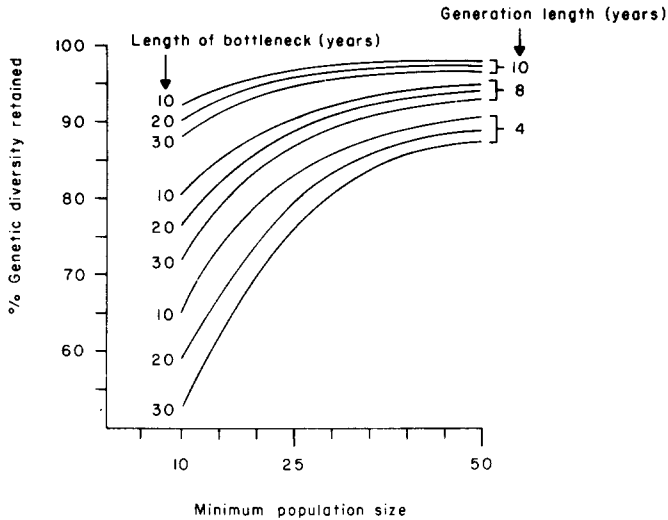
Fig. 8. The percentage of the original genetic diversity which would be retained in the present California sea otter population assuming various minimum population sizes, bottleneck lengths, and generation lengths, if it behaved as an ideal population.

suggests that either there were more than 50 animals in 1914 or that the growth rate of the population was not constant over time. Using a minimum population size of 50 and a generation length of eight years results in a theoretical loss of less than 10% in the ideal population, regardless of the length of the bottleneck (Fig. 8). Increasing the minimum population size to 100 would only increase the harmonic mean population size to 312; it can be seen from Fig. 5 that this would have little effect on the amount of genetic diversity lost.

We speculate that the effective population size is not less than 27% of the population size. This assumes a breeding sex ratio of one male to five females and that not more than 50% of the population is immature (Table 3). Under these assumptions the amount of genetic diversity retained would be 90% × 0·85 or 77%. This estimate is conservative because it assumes that heterozygotes have no selective advantage. Such heterozygote advantage is the rule in natural and laboratory populations (Wright, 1977; Soulé, 1980; Frankel and Soulé, 1981) and would result in the retention of even more of the genetic variation present in the original population.

Under any reasonable set of assumptions it seems likely that the California population of sea otters should have theoretically retained a

fair degree of the original genetic diversity. However, the predictions of theoretical population genetics have not, to our knowledge, been verified with respect to the history of any mammalian population. Studies of the genetic diversity existing in the present California sea otter population through electrophoresis and other more recently developed techniques (Jones, 1980), as well as comparisons with the Alaska population, are needed to substantiate our theoretical conclusion.*

A translocation of 25 to 50 otters for three to five years as recommended by Jameson *et al.* (1982) would probably still retain a large proportion of the genetic diversity presently existing in the California population after 40 years (Fig. 7). However, since the present California population has probably lost at least a small percentage of its original genetic diversity, it would be advisable to supplement the original translocation with a few additional animals from time to time. Migration or translocation of as few as one or two successfully breeding individuals per generation between the existing California population and the transplanted population would theoretically ensure that the two subpopulations would have the properties of a single interbreeding group and thus avoid any further loss of genetic diversity in the translocated population (Franklin, 1980).

Our conclusion that the California sea otter population probably retains a fair degree of the original existing genetic diversity should not be extended to other threatened or endangered species. In many of these species, populations have not only been reduced to a small fraction of their original size, as in the sea otter, but unlike the sea otter, have been maintained at low population levels for long periods of time and are thus likely to be substantially reduced in genetic diversity.

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* Preliminary studies carried out after completion of this manuscript have confirmed our prediction (Lidicker & McCollum, 1981; Ralls & Fisher, unpublished data).

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